

A Brief Review of the Genetics of Partly Colored Seed Coats in Common Bean

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All the partly colored seed coat patterns discussed in this review have their names, genotypes, and random amplified polymorphic DNA (RAPD) markers listed in Table 1, and the patterns are illustrated (graphic layout by Rachel Stevens) on the last two pages of the review. The seed coat patterns controlled by the *C* and *Stp* genes are not discussed in this paper.

Partly colored seed coat patterns are expressed only with the genotype *t/t*, the recessive genotype at Emerson's (1) *T* locus for *Totally* colored seeds. Today, these seeds are now usually referred to as self-colored seeds. The *t/t* genotype has a pleiotropic effect leading to white flowers and is epistatic to the *V* gene for purple flowers (1). The colored area of the seed coat can have any of the many hues possible for common bean (2), except for white, which is always the color of the non-colored area. Four additional genes control the size and shape of the colored seed coat pattern: *zonal* (*Z*), *bipunctata* (*Bip*), *limiter* (*L*), and the *J* gene. A third allele at *T*, viz., *t^{cf}*, permits the expression of partly colored seed coats without changing the flower color to white (3). But in otherwise equivalent genetic backgrounds, the restriction of colored area patterns due to *t^{cf}/t^{cf}* is not as severe as with *t/t* (Bassett, unpublished data). For example, *t^{cf} z t⁺* produces patterns ranging from self-colored to one similar to *expansa* (Fig. 1 without the fibula arcs), whereas *t z t⁺* produces the more restricted *virgarcus* pattern (Fig. 4). Similarly, *t^{cf} z t^{ms}* and another unidentified gene produce the two points pattern (Fig. 2) (Bassett, unpublished data), whereas *t z t^{ms}* produces a white seed. With genotype *t Z Bip J t⁺* the seed coat can be either self-colored (4) or have the *expansa* pattern (5), which is the same as the *minus* pattern (6, see Fig. 10 in that article). A newly discovered dominant acting gene, *Fibula arcs* (*Fib*), also affects patterning. With genotype *t Z Bip J t⁺ Fib* the seed coat has the *expansa* with fibula arcs pattern (Fig. 1), where *Fib* expresses the fibula arcs pattern and restricts slightly more the *expansa* pattern (Bassett, unpublished data).

The *Z* locus discovered by von Tschermak (7) controls several seed coat patterns reported in that article: *virgarcus* (*t z Bip J t⁺*) (Fig. 4), *piebald* (*t z^{sel}/z Bip J t⁺*) (Fig. 5), and *sellatus* (*t z^{sel} Bip J t⁺*) (Fig. 6). Lamprecht (8) removed the subscript 2 from von Tschermak's *Z*₂ locus symbol to re-designate it *Z*, and Bassett (9) assigned *Z* to the allele giving no pattern restriction and *z^{sel}* to the *sellatus* pattern allele. The genotype *t Z/z Bip J t⁺* has the highly variable seed coat pattern *ambigua* (Fig. 3), which was discovered by Schreiber (5). The degree of instability of *Z/z* *ambigua* pattern declines greatly with increasing homozygosity of the entire genome.

The inheritance of the *bipunctata* pattern with genotype *t z bip J t⁺* (Fig. 9) was reported simultaneously by Lamprecht (6) and Schreiber (5) and confirmed by Bassett (10). A third allele at *Bip*, viz., *bip^{ana}*, controls the *Anasazi* seed coat pattern (Fig. 7) with genotype *t z bip^{ana} J t⁺* (11). The genotype *t z bip^{ana} J t⁺* produces the *Anabip* pattern (Fig. 8), which is nearly as restricted as *bipunctata* (Fig. 9) (11).

The *J* locus was discovered to have interactions with *t* by Bassett (12, 13), where genotype *t Z Bip j t⁺* expresses the *marginata* pattern (Fig. 10). The same *marginata* pattern can also be expressed by the genotype *t Z L*, according to Schreiber (5). Genotype *t z Bip j t⁺* expresses white seed coat (14), as does *t z Bip J t^{ms}* (15); and when those two genotypes are crossed, the F₁ and F₂ progeny express only white seed coats (Bassett, unpublished data). Those

allelism test results give strong support to the hypothesis that *J* and *L* are allelic; but unlike the data demonstrating that the *z* and *d* (former symbol for the hilum ring factor) alleles are one and the same (14), the *j* and *I^m* alleles cannot be identical. For example, *t Z Bip j* expresses marginata (12, 13), whereas the *t Z Bip I^m* genotype expresses self-colored or expansa (15). Much additional research is needed to establish the details of a possible allelic series including *J* (same as *I^r*), *j*, *L* (*j^L* ?), and *I^m* (*j^m* ?), where the *J* symbol has precedence over *L*. Similarly, much additional research is needed to explore the hypothesis that the fibula arcs factor *Fib* can transform *t Z bip^{ma} fib* Anasazi into *t Z bip^{ma} Fib* marginata and transform *t z Bip J fib* virgarcus into *t z Bip J Fib* arcus (almost indistinguishable from weak virgarcus, Fig. 11) (Bassett, unpublished data).

The mutual independence of the genes *T*, *Z*, and *Bip* has been established repeatedly in previous literature cited above, e.g., (4, 5). Also, the independence of the genes *T*, *Z* and *L* has been established (5). Recently, the *Bip* locus was demonstrated to be independent of the *L* locus by means of the test cross *t z bip* (bipunctata) × *t z I^m* (white seed), which segregated in the *F*₂ for the virgarcus class, the expected class demonstrating non-allelism (Bassett, unpublished data). Therefore, there are at least four independent genes controlling expression of partly colored seed coat patterns, viz., *T*, *Z*, *Bip*, and *J* (Table 1).

The development of RAPD markers for genes controlling partly colored seed coat patterns has added important support to test-cross evidence for a number of discoveries. Examples are, 1) establishing *I^f* as a new allele at *T* (3), 2) confirming the allelism of *z* and *d* (14), and 3) establishing *bip^{ma}* as a new allele at *Bip* (11). RAPD markers for *T* were achieved first (16) and applied to the *I^f* discovery (3). Next, a RAPD marker for *Z* was applied to the establishment of allelism of *d* and *z* (14). Finally, RAPD markers for *Bip* were applied to the discovery of *bip^{ma}* (11). A RAPD marker for *L* has been developed (not shown in Table 1), but its application to the *J* and *L* allelism hypothesis is still a work in progress. Lab work to develop both coupling and repulsion RAPD markers for *Fib* and *fib*, respectively, is in progress. Development of a repulsion RAPD for *z* is in the planning stage. The only other genes (well supported by experimental data) playing a role in partly colored seed coats that have no molecular marker are the *circumlineatus* (*cl*) gene of Prakken (2) and the unidentified gene for the two-points pattern mentioned above.

References

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Table 1. Names and genotypes of partly colored seed coat patterns and RAPD markers for three of the four principal genes involved in pattern expression..

| Gene symbol | RAPD markers | Ref. no. | Linkage | | Partly colored patterns | | |
|-------------------------------------|-----------------------|----------|---------|-------|---|--------------------------|----------------------|
| | | | cM | Phase | Genotype | Name | Figures ^a |
| <i>T</i> | OAM13 ₁₃₅₀ | 15 | 2.5 | R | <i>t Z Bip fib</i> | Self-colored | |
| | OAM19 ₄₀₀ | 15 | 1.4 | R | <i>t Z Bip Fib</i> | Expansa with fibula arcs | 1 |
| | | | | | <i>t^{cf} z l^{ers} ?^b</i> | Two points | 2 |
| <i>Z</i> | OAM10 ₅₆₀ | 13 | 1.4 | C | <i>t Z/z Bip</i> | Ambigua | 3 |
| | | | | | <i>t z Bip</i> | Virgarcus | 4 |
| | | | | | <i>t z^{sel}/z Bip</i> | Piebald | 5 |
| | | | | | <i>t z^{sel} Bip</i> | Sellatus | 6 |
| <i>Bip</i> | OM9 ₂₀₀ | 10 | 5.4 | C | <i>t Z bip^{ana}</i> | Anasazi | 7 |
| | | | | | <i>t z bip^{ana}</i> | Anabip | 8 |
| | OJ17 ₇₀₀ | 10 | 6.0 | C | <i>t z bip</i> | Bipunctata | 9 |
| <i>J</i> (<i>l</i> ⁺ ?) | | | | | <i>t Z j</i> (or <i>t Z L</i>) | Marginata | 10 |
| | | | | | <i>t z l⁺/l^{ers}</i> | Weak virgarcus (Arcus) | 11 |
| | | | | | <i>t z J/j</i> | See footnote c | |
| | | | | | <i>t z j</i> (or <i>t z l^{ers}</i>) | White | |
| | | | | | <i>T Z j</i> | Margo | 12 |
| | | | | | <i>T z j</i> | Margo "d" | 13 |

^aThe figures appear on the following two pages.

^bAn unidentified gene controls the expression of two points pattern on the otherwise white seed produced by *t z l^{ers}*.

^cThe pattern produced by *t z J/j* is different and not illustrated and may be described as "weak bipunctata," i.e., an otherwise white seed having two tiny, pale gray dots, one at the raphe and the other at the micropyle. Schreiber (5) described the expression of *t z l⁺/L* as white, but that genotype (derived from his 'Thuringia' source) grown at Gainesville expressed the "weak bipunctata" pattern of *t z J/j* (Bassett, unpublished data).

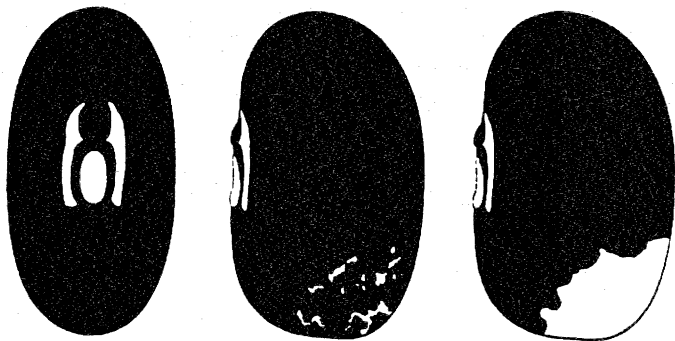


Fig.1

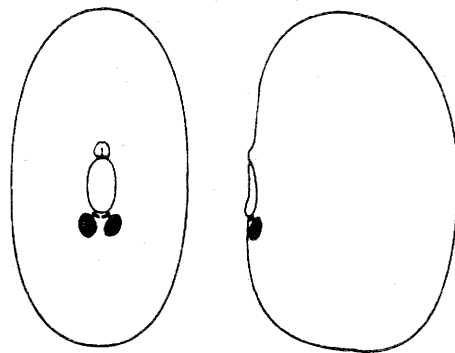


Fig. 2

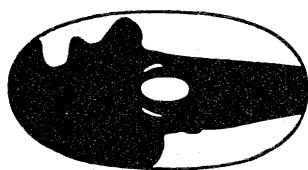
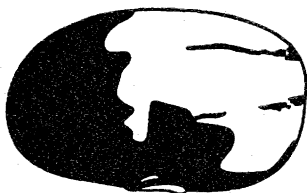


Fig. 3

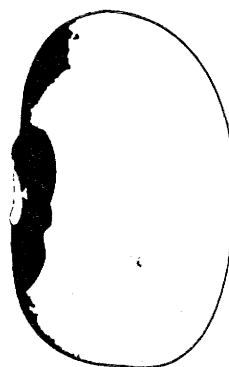
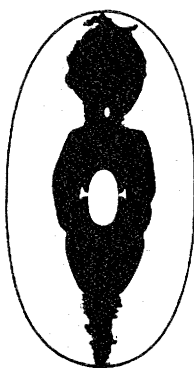


Fig. 4



Fig. 5

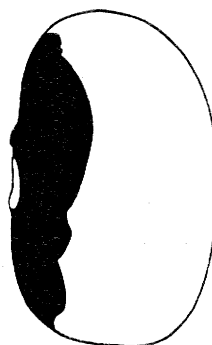
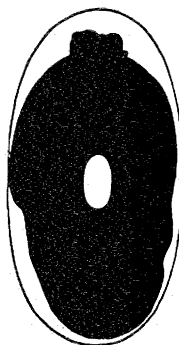


Fig. 6

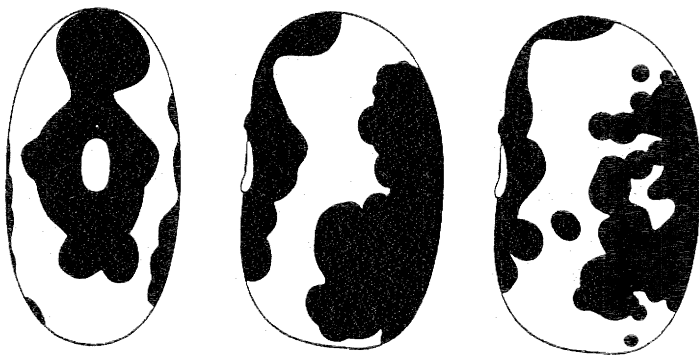


Fig. 7

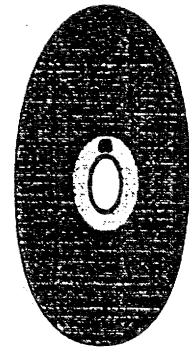


Fig. 12

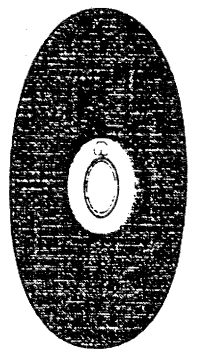


Fig. 13

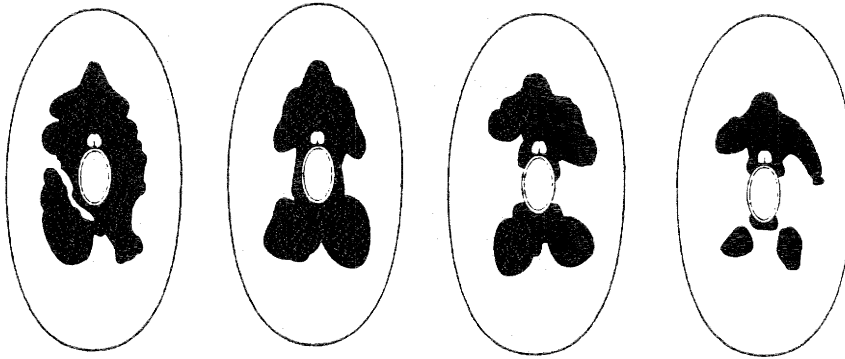


Fig. 8

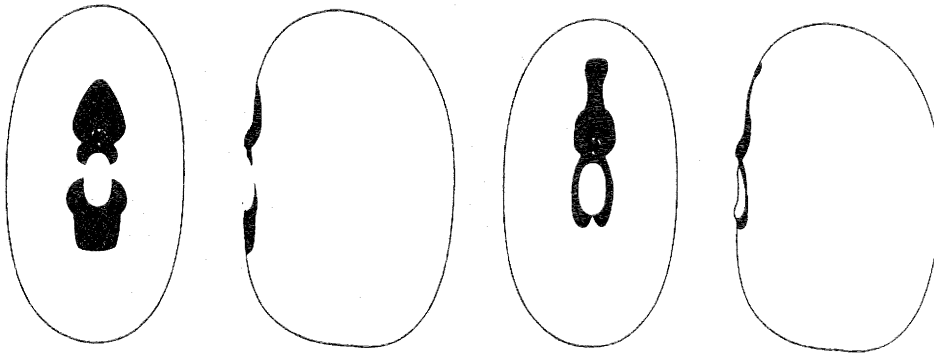


Fig. 9

Fig. 10

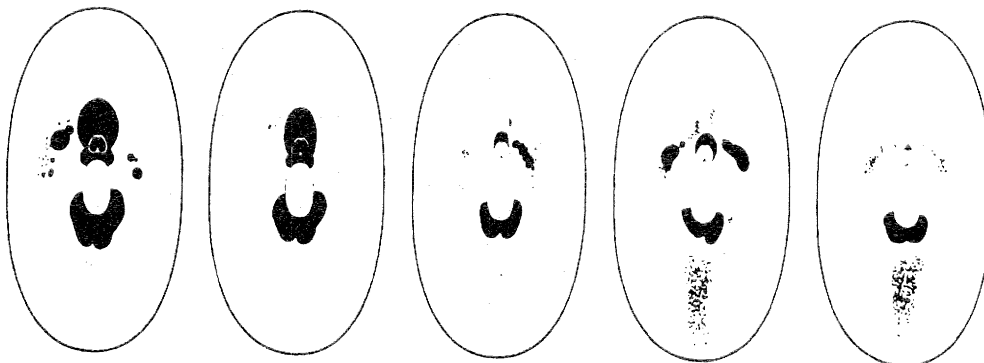


Fig. 11